## ADDENDUM III

# Ecosystem engineers stabilize sand bank systems: *Owenia fusiformis* aggregations as ecologically important microhabitat

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## Abstract

Ecosystem engineers modify the physical environment and have profound effects on ecosystem functioning and on local biodiversity. Yet, in soft bottom marine environments, they have rarely been included in hydrodynamic studies or in management strategies. The lack of quantified stabilization potential and ecological impact are, respectively, the main reasons for not including ecosystem engineers. The present study evaluates the ecosystem engineering capacity of the tube dwelling polychaete *Owenia fusiformis*. The ecological implications of aggregations of this species are investigated using a long term dataset (1994-2006). Results show that its presence has significant implications for species richness and species density. These aggregations are further investigated with different remote sensing tools. *Owenia fusiformis* is able to stabilize sand dunes that normally migrate 12 m a year. Specific biological characteristics explain the stabilizing effects in a highly dynamic environment. Our results confirm the need to pay attention to biota in sediment transport modelling. We conclude that *O. fusiformis* creates an important marine system which can be investigated with sensing techniques. These techniques can therefore be used to visualize hotspots of biodiversity, to quantify their biogeomorphological impacts and to underpin ecosystems based management in the marine environment.



## Key words

Ecosystem engineer, remote sensing, sediment stability, side scan sonar, multibeam sonar, *Owenia fusiformis*, ecosystem management

# Introduction

The relationship between structure and functioning is fundamental in ecosystem science (Levin, 1998). The structural complex framework provided by emergent features constitutes an important organizing aspect and is critical to the functioning of many ecosystems (Jones et al., 1994). Biogenic structures in marine ecosystems that reach a few centimetres into the water column can therefore have a profound effect on the structure and functioning of marine ecosystems. These systems are heavily used by a variety of taxa, including post-settlement juveniles of commercially important fish species (Watling and Norse, 1998). Anthropogenic activities can cause deleterious impacts on the seabed environment, which identifies the need to identify and map different types of benthic habitats and their associated biological communities. As the protection of vulnerable, rare or ecologically important areas is now widely recognized (Pickrill and Todd, 2003), there is a growing need for improved understanding of seafloor ecosystems to facilitate sustainable marine management and environmental monitoring.

The relationship between structure and functioning owing to biotic-abiotic interactions was conceptualised in the idea of 'ecosystem engineering' (Jones *et al.*, 1994, 1997, Wright and Jones, 2006). Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing state changes in biotic or abiotic materials. In doing so they modify, maintain and/or create habitats (Jones et al., 1994). By reshaping the landscape, ecosystem engineers change the abiotic context upon which biotic interactions heavily depend (Byers et al., 2006). The value of the ecosystem-engineering concept, therefore, lies in its ability to formalize interactions among organisms that are mediated by the physical environment (Wilby, 2002).

The ecological effects of habitat structuring organisms are well described for all kinds of marine environments: coral reefs (e.g. (Holbrook et al., 1990), Darwin mounds (Van Gaever et al., 2004), kelp forests (e.g. (Steneck et al., 2003), ascidians (Castilla et al., 2004), sea grass meadows (e.g. (Alfaro, 2006, Hovel *et al.*, 2002), mussel banks (Ragnarsson and Raffaelli, 1999), oyster beds (Lenihan, 1999) and polychaete tubes (Callaway, 2006, Van Colen *et al.*, 2008). Recently, a descriptive and correlative data study (Rabaut et al., 2007) illustrated the ecological importance of the ecosystem engineer *L. conchilega* in shallow soft-bottom areas.

The habitat modifying ability of this tube building polychaete creates and regulates refuge for species, alters the interactions between local species and changes the physical environment. This species has the capacity to double the biodiversity in the richest soft-sedimented macrobenthic habitat of the Belgian part of the North Sea (BPNS) (*i.e.* the *Abra alba* community) (Van Hoey et al., 2004). The effect of this species on biodiversity has been described extensively (Callaway, 2006, Carey, 1987, Dittmann, 1999, Féral, 1989, Rabaut *et al.*, 2007, Van Hoey, 2006, Zühlke *et al.*, 1998) and the species was recently defined as a reef builder (Rabaut *et al.*, 2009b). Furthermore, several studies describe in detail how *L. conchilega* affects the abiotic environment (Braeckman *et al.*, accepted, Forster and Graf, 1995).

The tube building polychaete, *Owenia fusiformis*, occurs in the same macrobenthic community (*Abra alba – Kurtiella bidentata*). *Owenia fusiformis* is a thin cylindrical, segmented worm, up to 10 cm long, that lives in a tough though flexible tube buried in the sand (Pinedo et al., 2000). The tube is composed of sand grains or shell fragments glued together in an overlapping, imbricate fashion. The tube is slightly longer than the worm and its top can protrude to up to two centimetres from the surface. Although several authors suggest that tubes of *O. fusiformis* mostly protrude above the sediment surface (Eckman *et al.*, 1981, Fager, 1964), there is, in some cases, still some uncertainty on the position of the tubes in the sediment, as recently discussed by Noffke et al. (2009). The species has an adult life span of three to four years (Menard et al., 1989), as opposed to *L. conchilega* which has a lifespan of about one year (Van Hoey, 2006). The species is widely distributed in coastal regions throughout North-Western Europe, the Mediterranean, the Indian Ocean and the Pacific and occurs in fine to coarse sediments, reaching only high densities in finer sediments (Pinedo *et al.*, 2000, Somaschini, 1993). There is little known about the formation of high density patches and their physical characteristics. The mechanisms of physical patch formation are certainly different compared to *L. conchilega*, as the tube is shorter and the organisms have a longer lifespan. Despite its wide distribution and the formation of aggregations, the ecological effects of this species have received little attention until now. Furthermore, the biotope seems to occur in sheltered areas with a high load of organic matter (pers. obs.).

As the marine environment proves difficult to access, remote sensing is taking up an ever more important role in the investigation of the structure and functioning of marine

landscapes (Diaz *et al.*, 2004, Kenny *et al.*, 2003, Mayer, 2006). Remote sensing techniques permit to improve the knowledge of the marine biodiversity and more specifically, its spatial distribution in a cost-effective manner (Larsen et al., 2007). Side-scan sonar still remains the undisputed remote sensing tool for small object detection (Blondel and Murton, 1997, Brissette and Clarke, 1999) and has been used to detect emergent biota and to characterise small-scale patchiness within ecological valuable areas (Degraer *et al.*, 2008a). These authors departed from the existing ecological knowledge on *L. conchilega* aggregations and provide evidence that the biogenic mounds created by this species can be visualised using side-scan sonar techniques. Nevertheless, the technology of multibeam sonar systems has rapidly evolved since the last decade. These systems make it possible to map backscattering strength, together with detailed bathymetry, substantially improving the capability of sonars to discriminate different types of seafloor habitats (Dartnell and Gardner, 2004, Kostylev *et al.*, 2003, Wilson *et al.*, 2007).

Furthermore, biota can affect local sediment transportation and stabilize or destabilize the environment. Individual structures on an otherwise smooth sea bed ('isolated roughness elements', in hydrodynamic terms) are known to cause local scour by deflecting fluid of relatively high momentum toward the bed. Such scour is seen around animal tubes (Gage, 1977). It is widely believed that animal tubes stabilize sediments by altering the character of near-bed flow. In some cases, the region of maximum turbulent kinetic energy and shear stress production occurs away from the bed (this is the so-called "skimming flow") (Morris, 1950). "Skimming flow" may therefore occur above the tops of *O. fusiformis* tubes and have a stabilizing effect on the dynamic sand bank system.

In the present study we hypothesize that *O. fusiformis* reshapes the marine environment by profoundly changing the abiotic context. The aim of this study is to investigate the effect on the abiotic sand bank system as well as the consequences of this stabilizing effect for the associated species community. The combination of different remote sensing techniques and biological samples makes it possible to study the relationship between the structure and functioning of a specific ecosystem engineered habitat.

# Material and Methods

## *Study area*

The study area covers a transect of the BPNS situated in the Southern Bight of the North Sea, close to the Belgian coast (Fig. 1). This shallow area (max. 35 m depth) consists of several sandbank systems, oriented more or less parallel to the coast. The characteristic geomorphologic and sedimentological diversity of these soft-bottom habitats is directly responsible for the high biological diversity and richness, reflected in a mosaic of several distinguishable macrobenthic communities (Degraer *et al.*, 2008b, Van Hoey *et al.*, 2004). For the remote sensing measurements, the area north of the Vlakte van de Raan within the Belgian coastal zone (51° 30'N , 3° 6'E) (Fig. 1: rectangular area) has been targeted for this investigation. The location is about 16 km offshore from the harbour of Zeebrugge, close to the Belgian-Dutch border. Depth ranges between 15 and 24 m relative to Mean Lowest Low Water at Spring tide (MLLWS). The area encompasses a tidal swale and the landward slope of a sandbank (Fig. 1). Hydrodynamics are mainly tidally-driven; nevertheless, wind and density currents can be important. The average current velocity in the study area is 0.3 m/s during ebbing tide, increasing to 0.8 m/s during flood tide (Lanckneus et al., 2001). In this area, the residual current is flood-dominated (Fettweis and Van den Eynde, 2003) while the bedload transport is ebb-dominated (Du Four and Van Lancker, 2008). Very-large dunes *sensu* Ashley (1990) of 2 to 3 m occur in this area, with wave lengths of 100 to 500 m.

## *Biological data and analyses*

Data, gathered on the BPNS, over a period of 11 years (October 1994 until November 2006), were selected on the basis of habitat classification, which takes into account sedimentological characteristics and bathymetrical information. A data set of 314 macrobenthic samples was submitted to analysis (Figure 1). This subset of samples was selected from shallow locations (<25 m according to MLLWS level) at which the fine sediment fraction was the largest, as sediment characteristics are known to determine macrobenthic species occurrence (Van Hoey et al., 2004).

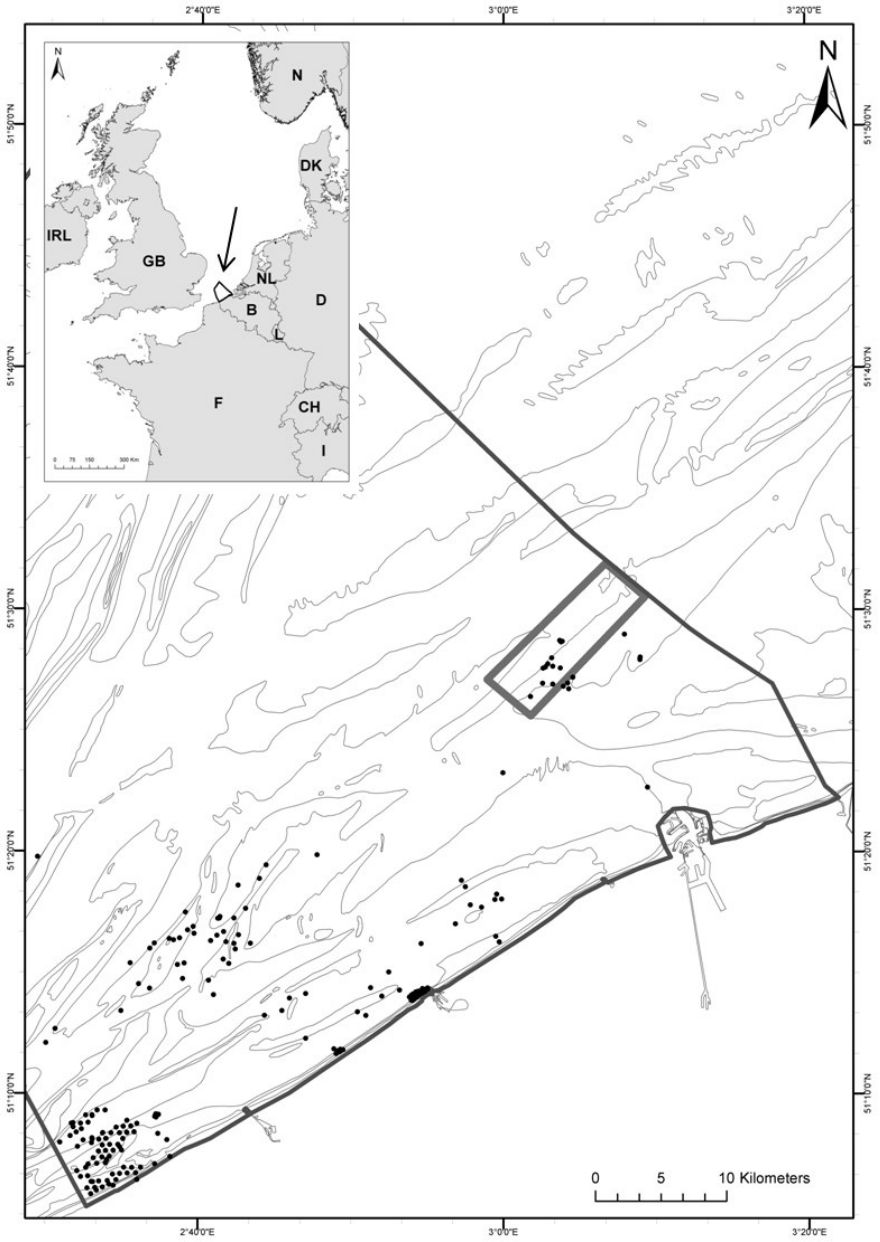


*Figure 1. Position of the Belgian part of the North Sea (BPNS) (inset); Coastal zone of the BPNS with the 314 sample locations for biological analyses. Depth contours of 10 m and 20 m are visualised. Indication of the location where remote sensing measurements were performed (area North of Vlakte van de Raan; rectangle).*

To test the impact of *O. fusiformis* as a ecosystem engineer, samples were selected based on specific median grain size values (125-250 µm); furthermore, samples with *L. conchilega* densities exceeding 10% of the *O. fusiformis* density, were removed in order to exclude the bias of the known bio-engineering *L. conchilega* (Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008). All samples were collected with a Van Veen grab of 0.1 m² surface area and sieved alive through a 1 mm mesh-sized sieve. Macrofauna was identified to the lowest possible taxonomic level (further referred to as species) and subsequently counted. Species abundance data were standardised to a total number of individuals per m².

In order to study the possible change in benthic community composition as a consequence of the presence of *O. fusiformis* tubes, samples were divided into 4 classes: (0) samples without tubes and samples with *O. fusiformis* densities ranging from (1) 1-30 ind $m^{-2}$, (2) 31-150 ind $m^{-2}$, and (3) > 150 ind $m^{-2}$, further referred to as density groups.

The quantitative faunistic data were analysed using a combination of multivariate and univariate methods. The benthic community structure was analysed with the PRIMER v6 statistical package (Clarke and Warwick, 2001). Non-parametric multidimensional scaling (MDS) and analysis of similarity (one-way ANOSIM) were used to describe (dis)similarities between benthic faunal communities of *O. fusiformis* sites and sites where *O. fusiformis* did not occur. The MVDISP algorithm of the PRIMER v6 software was used to quantify the variability in each density class and to calculate the Index of Multivariate Dispersion (IMD). This comparative Index contrasts the average rank of the similarities among samples of a certain density class with the average rank of other density class sample groups (Clarke and Warwick, 2001). With the SIMPER program the (dis)similarity between the communities and the percentage contribution of each species to the similarity within and dissimilarity between communities was examined. Species richness for different *O. fusiformis* density classes was calculated and presented by total number of species (S) and Margalef's index (d) which takes into account the given number of individuals (Clarke and Warwick, 2001). Differences between density groups regarding the number of individuals (N), species richness (S) and Margalef's index (d) were tested with a general linear model (SAS software). Homogen eity of variances was tested (Levene's test) and differences between different density classes were tested with the post hoc Tukey test.

In order to identify species possibly associated with the presence of *O. fusiformis*, four criteria were applied (Rabaut et al., 2007). The Indicator Species Analysis (ISA, Pcord4 programme) was carried out and an association degree (the percentage of occurrence of a species in samples with *O. fusiformis*, relative to the total presence of that species in all samples) was calculated. Apart from this, the Mann-Whitney U test was used to compare abundances of these species between samples with and without *O. fusiformis*. Finally, the correlation of the density of *O. fusiformis* tubes with individual species abundances was tested with the Spearman Rank correlation analysis. A species was defined as positively associated with *O. fusiformis* when (1) a significant indicator value was attributed, (2) the association degree was more than 50%, (3) species density significantly differed between samples with and without *O. fusiformis* and if (4) a positive and significant correlation with the density of *O. fusiformis* was found. Based on these results species were ranked according to a summation of the indicator value and the association degree.

## *Multibeam bathymetry*

Multibeam sonar was selected to detect small-scale *O. fusiformis* patches, to define their spatial extent and to show the influence of *O. fusiformis* aggregations on bedform stability.

Multibeam imagery was acquired in February and November 2006 and in February, October and November 2007, using a Kongsberg Simrad EM1002 multibeam echosounder (*RV Belgica*) (Fig. 2). In total, 33 km² was surveyed. The EM1002 provides high-resolution bathymetric data, with up to 111 receive beams of 2° (athwart) x 3.3° (fore-aft) width. It works at a nominal frequency of 95 kHz with a ping-rate of around 4 to 6 Hz. The data are real-time corrected for the roll and heave using a Seatex MRU 5 motion sensor and for the heading using an Anschütz Standard 20 gyrocompas. The geographic co-ordinates are provided by a Thales Aquarius 02 GPS positioning system with a theoretical precision of 10 mm. The soundings are tide-corrected using the specific M2 tidal reduction method for the Belgian coastal zone (Van Cauwenberghe et al., 1993) and referenced to the level of MLLWS. In water depths less than 30 m, the depth measurement accuracy is estimated to be around 10 cm RMS or 0.2 % of the depth (Kongsberg-Simrad, 1999-2001a). Post-processing was done using the software packages Neptune (Kongsberg-Simrad, 1999-2001b) and Fledermaus and

resulted in digital terrain models (DTM) with a 1-m or 2-m grid resolution. All information was spatially referenced in ArcGIS 9.3.

To define the elevation of the individual patches, cross-sections aligned in a NW-SE direction were generated from the October 2007 DTM (Fig. 2). To investigate bed form migration, changes in the crest positions of the dunes were determined based on cross-sections aligned in a SW-NE direction (transverse to the dunes) and generated from all DTMs.

To validate the multibeam imagery, 117 ground truth samples were taken in within the study area (Fig. 2) of which *Owenia fusiformis* densities were determined.

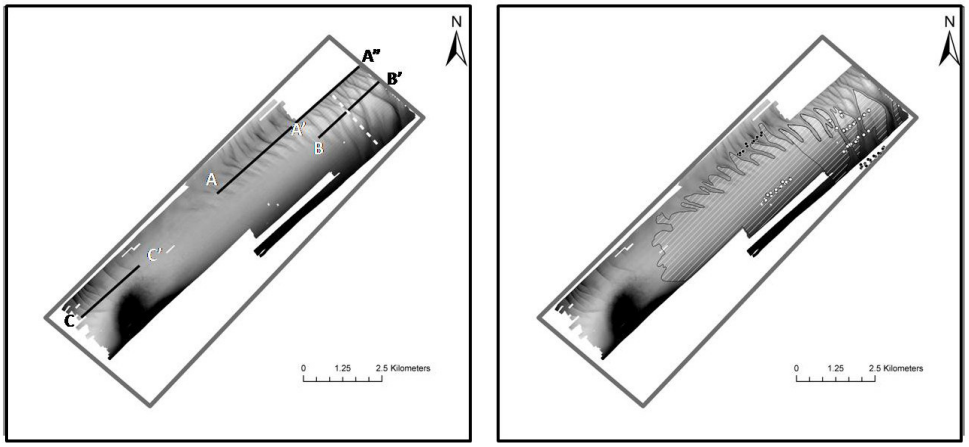


*Figure 2. Study area north of the Vlakte van de Raan, where remote sensing imagery was acquired. Left: area with multibeam echosounder measurement, indication of investigated transects (black lines) and indication of a side scan sonar trackline (white dotted line); Right: delineation of the zone where* Owenia fusiformis *is observed (dashed area) and position of ground truth samples inside (white dots) and outside (black dots) the* O. fusiformis *area.*

## *Side-scan sonar imagery*

Side-scan sonar was selected to obtain a detailed view of the individual *O. fusiformis* patches. The imagery is a reflection of the acoustic energy that is backscattered from the seafloor and is displayed in different grey levels. Blondel and Murton (1997) explain the operational procedures and technical constraints of side-scan sonar technology.

Very high resolution side-scan sonar imagery was acquired in November 2007, using a Klein 3000 series, which was deployed at a frequency of 445 kHz. The sonar was towed at a speed of 4 knots with an altitude of 3-4 m above the sea bottom along a NW-SE transect (Fig. 2). The sonar range was set at 50 m. Positioning was done using CSI Wireless Inc. DGPS. All data were recorded digitally using ISIS acquisition software (Triton-ELICS). The processing (at 25 cm resolution) and mosaicing was performed with ISIS and Delphmap. Corrections for the distance of the fish to the seabed (the slant range), lay-back/offset and vessel speed were taken into account.

Finally, the images were exported as Geotiffs for further interpretation. All information was spatially referenced in ArcGIS 9.3.

# Results

## *Biological implications of* Owenia fusiformis

According to the one-way ANOSIM analysis, the macrobenthic community around *O. fusiformis* tubes is significantly different from the community in *O. fusiformis* free areas (R= 0.198; p = 0.001) (Table 1). A dissimilarity value of 82.3 was found between samples with and without *O. fusiformis*. Dissimilarities between density classes are relatively high, with the 0-density class being most distinguishable from all other classes. ANOSIM results reveal significant differences between all classes except between class 1 and class 2 (Table 1).

Differences in dispersion were investigated using the MVDISP algorithm. The highest variability was found in the samples without *O. fusiformis* (Dispersion Factor Value 1.019) while lowest variability occurred in the samples with highest *O. fusiformis* densities (Dispersion Factor Value 0.354). For each density class, the indices of multivariate dispersion (IMD values) show that similarities among samples of the concerned class are higher than the similarities among samples of a lower density class. The community structure is visualized in a 2-dimensional ordination graph constructed by the MDS-analysis (stress 0.24) (Fig. 3) and shows how the different density groups are organized. IMD values and MDS-analysis indicate that *O. fusiformis* expands the realized niche of several species and creates a so-called "Babushka" type of community structure (sensu Rabaut et al, 2007).

*Table 1. Results of the global and pairwise ANOSIM and SIMPER analysis for differences between the macrofauna community composition of* Owenia fusiformis *patches with different classes of densities (1-3) and* O. fusiformis*-free patches (0).*

| | R | p | Dissimilarity |
|---|---|---|---|
| **Presence/Absence** | 0.198 | 0.001 | 82.3 |
| | | | |
| **Density classes** | | | |
| *Global test* | 0.124 | 0.001 | |
| *Pairwise test* | | | |
| 0 - 1 | 0.12 | 0.002 | 81.24 |
| 0 - 2 | 0.098 | 0.034 | 80.89 |
| 0 - 3 | 0.283 | 0.001 | 85.14 |
| 1 - 2 | 0.004 | 0.401 | 67.77 |
| 1 - 3 | 0.286 | 0.001 | 73.78 |
| 2 - 3 | 0.336 | 0.001 | 67.74 |

Average macrobenthos densities (mean ± SE) of 2464 ± 289 ind $m^{-2}$ were found in the presence of *O. fusiformis*, while significantly lower densities of 1335 ± 153 ind $m^{-2}$ were found in samples without *O. fusiformis* ($p = 0.0056$). Species richness differed significantly ($p < 0.0001$) for presence-absence groups. The highest macrobenthic density was found in density class 1, while the highest species richness (as reflected in S and d) occurred in class 2 (Table 2). For density classes, the group of samples without *O. fusiformis* differed significantly from all other density classes. However, none of the density classes with *O. fusiformis* could be distinguished significantly on the basis of N, S or d.

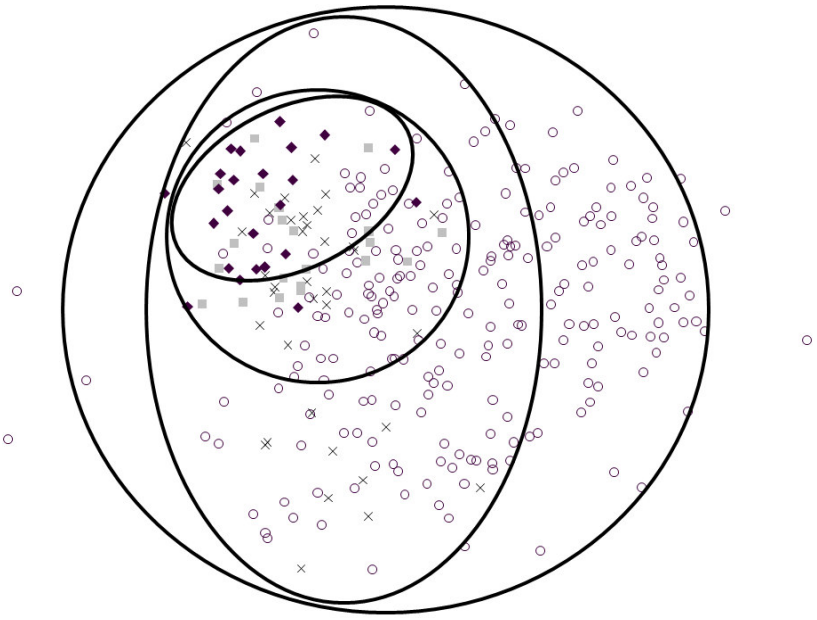

*Figure 3. Two-dimensional MDS ordination plot of similarities between species assemblages of different density classes of* Owenia fusiformis *aggregations (classes 1-3, respectively crosses, filled gray squares, filled diamonds) and* O. fusiformis *-free samples (open dots) (using Bray-Curtis similarity measure of square root transformed data). The 'babushka" like organisation of the samples indicates that* O. fusiformis *restructures the species assemblage by expanding the realized niche of several species.*

*Table 2. Abundance (N) and Species richness for presence/absence samples and for different* Owenia fusiformis *density classes, represented by average number of species per sample in each density class (S) and by Margalef's index (d). Species richness increases with increasing* O. fusiformis *densities, except for the highest* O. fusiformis *density class. The highest macrobenthic density is found when* O. fusiformis *is present (maximum N within presence group found in class 1).*

| Presence/Absence | N | S | d |
|---|---|---|---|
| 0 | 1335 | 10.76 | 1.49 |
| 1 | 2464 | 19.10 | 2.40 |

| Dens class | N | S | d |
|---|---|---|---|
| 0 | 1335 | 10.76 | 1.49 |
| 1 | 3766 | 18.86 | 2.39 |
| 2 | 2216 | 21.62 | 2.71 |
| 3 | 2228 | 17.25 | 2.14 |

135 macrobenthic species (*O. fusiformis* excluded) were recorded in this study of which 19 were found to be positively associated with *O. fusiformis* (*i.e.* 14%) (Table 3). The three most associated polychaetes are *L. conchilega*, *Pholoe minuta*, *Notomastus latericeus*. For bivalves, *Abra alba* and *Kurtiella bidentata* seem to be clearly present in higher densities in areas with *O. fusiformis*. Relatively few amphipods appear in the list of positively associated species (e.g. *Ampelisca brevicornis* and *Melita sp*.). Echinoderms appear in the top ranking of associated species with *Ophiura sp*. on number one. Finally, the burrowing sea anemone *Edwardsia timida* is indicative for areas where *O. fusiformis* occurs. For each species, the relative contribution to the dissimilarity is indicated in the table (Table 3).

## *Abiotic implications of* Owenia fusiformis

The digital terrain model, based on the multibeam echosounder recordings, reveals the presence of a patchy micro-habitat (Fig. 4). Ground truth samples were divided into two groups: 83 samples were taken in areas showing the patchy environment; 36 sampling locations were selected in an area without patches. In 93% of the samples of the first group, *O. fusiformis* was present, while for the ground truth samples outside the patches only 19% of the samples held *O. fusiformis*. Moreover, average densities (ind/m² +/- SE) were respectively 582.99 +/- 56.75 and 3.79 +/- 1.79. The patches are observed along an elongated band of approximately 2 km wide, following the overall bathymetry of the swale. On the landward slope of the sandbank, they occur in between the very-large dunes. Surface area of the patches varies substantially and ranges from 0.6 m² up to 12 m² (Fig. 5). The individual patches vary from circular to elongated and their elevation varies between 15 cm and 40 cm (Fig. 6). Side-scan sonar imagery also reveals the patchiness of the *O. fusiformis* aggregations (Fig. 4). Medium to relatively high reflectivity acoustic facies characterise the patches. The texture varies from slightly grainy to grainy.

The very large dunes, aligned in the NW-SE direction, have a wavelength between 150 and 450 m with an elevation ranging between 1.5 and 3 m. They exhibit an asymmetric cross-section with their steeper lee-slope mainly oriented towards the southwest, indicating net sand transport in that direction. Most of them have superposed small dunes on their stoss side. The wavelength of the small dunes varies between 0.10 and 0.15 m with an elevation ranging between 0.15 and 0.2 m.

*Table 3. Rank list of the associated species. Species are ranked based on the summation of the indicator value (ISA) and the association degree. Mann-Whitney U indicates the significance level of differences in abundances of the species between samples with and without* Owenia fusiformis*. The Spearmen Rank R-value indicates the correlation of the density of* O. fusiformis *tubes with individual species abundances. The last column represents SIMPER results, indicating the relative contribution of a species to the dissimilarity between samples with* O. fusiformis *and samples without.*

| | ISA | | Assoc degree | Mann-Whitney U-test | Spearman rank | SIMPER |
|---|---|---|---|---|---|---|
| | indicator value | p | (%) | p | R (p<0.05)) | % contribution |
| ***Positively associated*** | | | | | | |
| *Ophiura sp.* | 63 | 0.001 | 57 | 0.000000 | 0.587396 | 4.72 |
| *Lanice conchilega* | 15 | 0.001 | 100 | 0.047012 | 0.409976 | 0.32 |
| *Pholoe minuta* | 32 | 0.001 | 82 | 0.000016 | 0.499130 | 0.88 |
| *Notomastus latericeus* | 49 | 0.001 | 63 | 0.000000 | 0.480938 | 2.15 |
| *Edwardsia timida* | 20 | 0.001 | 89 | 0.010635 | 0.424169 | 1.16 |
| *Acrocnida brachiata* | 16 | 0.001 | 93 | 0.035555 | 0.338578 | 0.4 |
| *Nereis sp.* | 45 | 0.001 | 62 | 0.000000 | 0.456615 | 1.21 |
| *Ampelisca brevicornis* | 21 | 0.001 | 82 | 0.005550 | 0.371184 | 0.51 |
| *Sthenelais boa* | 26 | 0.001 | 74 | 0.000360 | 0.384294 | 0.65 |
| *Actinaria sp* | 41 | 0.001 | 55 | 0.000002 | 0.351610 | 2.35 |
| *Oligochaeta sp* | 42 | 0.001 | 53 | 0.000001 | 0.341871 | 2.24 |
| *Melita sp* | 20 | 0.001 | 73 | 0.005924 | 0.354943 | 0.67 |
| *Pectinaria sp* | 35 | 0.001 | 55 | 0.000280 | 0.295016 | 1.04 |
| *Venerupis senegalensis* | 17 | 0.001 | 71 | 0.031815 | 0.259206 | 0.58 |
| *Phyllodoce (A.) maculata* | 32 | 0.001 | 50 | 0.000433 | 0.274872 | 1.26 |
| *Nassarius reticulatus* | 27 | 0.001 | 52 | 0.002206 | 0.235659 | 1.16 |
| *Eumida sanguinea* | 22 | 0.001 | 57 | 0.002270 | 0.293931 | 0.72 |
| *Glycera alba* | 21 | 0.001 | 56 | 0.018423 | 0.222493 | 0.61 |
| *Ophiura juv* | 22 | 0.001 | 53 | 0.014482 | 0.268687 | 1.5 |
| ***Negatively associated*** | | | | | | |
| *Bathyporeia sp* | 1 | 0.002 | 11 | 0.002297 | -0.225407 | 1.61 |
| *Urothoe poseidonis* | 3 | 0.006 | 11 | 0.001241 | -0.229499 | 1.42 |
| *Nephtys cirrosa* | 4 | 0.001 | 12 | 0.000000 | -0.362687 | 3.27 |
| *Spio sp.* | 3 | 0.002 | 18 | 0.016994 | -0.174198 | 2.23 |

The very large dunes in the northern and central part, where the *O. fusiformis* aggregations occur, did not migrate during the two subsequent years (Fig 6, profiles A-A'-A'', B-B'), while for the southern part of the study area, comparison of dune crests positions of the very-large dunes demonstrate that the dunes migrated 12 m towards the SW between February 2006 and November 2007 (Fig 6, profile C-C').

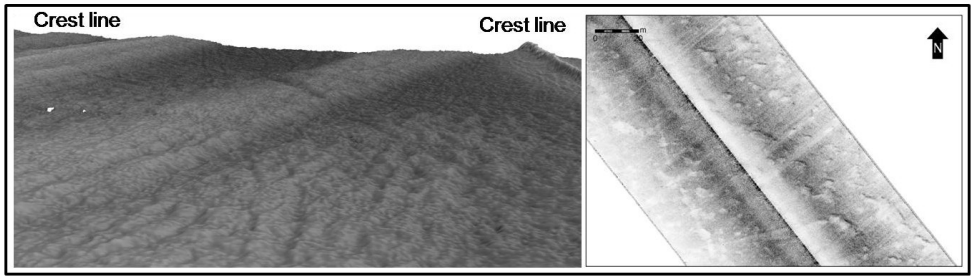


*Figure 4. Visualisation of patches formed by* Owenia fusiformis *aggregations, visualized with MBES (left, 3D), side scan sonar imagery (right, plan view).*

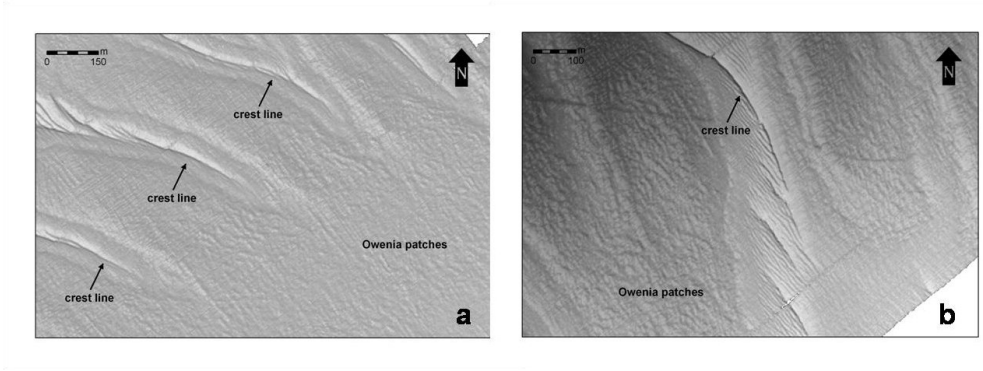


*Figure 5. On the landward slope of the sandbank,* Owenia fusiformis *patches occur in between the very-large dunes (in between crest lines): (a) general view and (b) detail. Surface area of the patches varies substantially and ranges from 0.6 m² up to 12 m².*

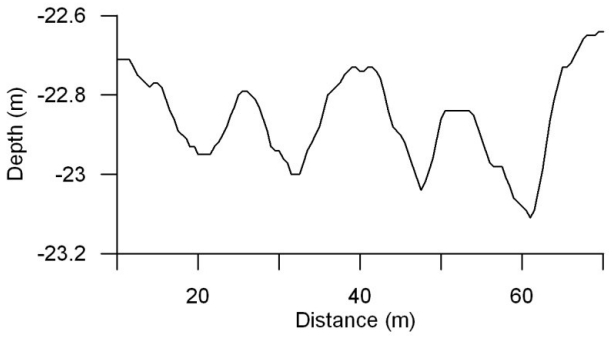


*Figure 6. Cross section indicating heights. Small scale elevation differences represent* Owenia fusiformis *patches. Their height varies between 15 cm and 40 cm.*

Finally, sediments accumulate over the whole dune area in the southern part, while in the other parts sediments accumulate only in the troughs, in-between the dunes (Fig. 7).

# Discussion

## *Biotic implications of* Owenia fusiformis

*O. fusiformis* is a strong ecosystem engineer. The two-dimensional ordination graph and the multivariate dispersion analysis demonstrate that *O. fusiformis* modulates its environment. The species does not create its own community, but structures the *A. alba – M. bidentata* community by expanding the realized niche of several species. This ecosystem engineering effect is very similar to the effect of *L. conchilega*, another tube dwelling polychaete of the same macrobenthic community (Rabaut et al., 2007). This kind of structuring the existing community is also referred to as the "babushka" like organization. The MVDISP results show an increasing dispersion of samples with decreasing *O. fusiformis* densities, which suggest a more stable environment when densities of *O. fusiformis* increase (Clarke and Warwick, 2001). However, *O. fusiformis* is not as strong an ecosystem engineer as *L. conchilega*. This is reflected in a lower relative increase of both average macrobenthic density (factor 5 for *L. conchilega*, factor 2 for *O. fusiformis*) and species richness (factor 3 versus factor 2). Moreover, the apparent "babushka" organization on community level is not reflected in a change of species richness and abundance over density classes of *O. fusiformis*. For these biological characteristics, the presence of *O. fusiformis* seems to be of importance, rather than the densities in which the species is present. The rank list of species shows species that prefer high to very high mud contents such as *Pholoe minuta* (Fauchald et al., 2009), *Notomastus latericeus* (Fauchald and Bellan, 2009) and *Ophiura sp.* (Stöhr and Hansson, 2009). The stable microhabitat created by *O. fusiformis* locally reduces currents (*cf.* "skimming flow"), which increases the mud content in this sheltered habitat. Other species like *Edwardsia timida* are known to occur in sheltered localities in shallow sublittoral areas (Wilson, 2007), which explains the high preference for the biogenically created habitat of *O. fusiformis*.

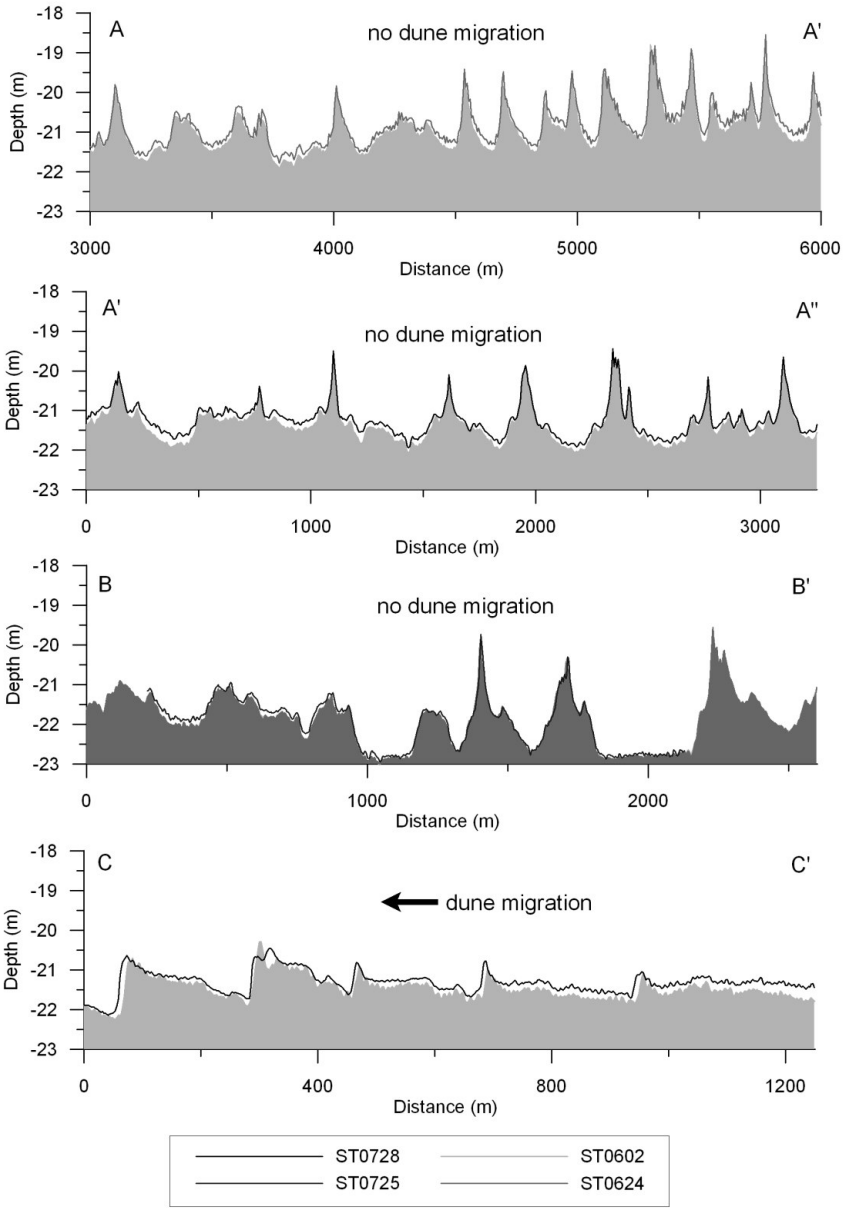


*Figure 7. Dune migration. Dunes in the northern and central part, where the* Owenia fusiformis *aggregations occur, did not move during the same time span (profiles A-A'-A'', B-B') while for the southern part of the study area, comparison of dune crests positions of the very-large dunes demonstrate that the dunes migrated 12 m towards the SW between February 2006 and November 2007 (profile C-C'). Note that sediments accumulate over the whole dune area in the southern part, while in the other parts sediments accumulate only in the troughs, in-between the dunes.*

Unlike *L. conchilega*, there are no species present that directly depend on the tubes of *O. fusiformis*. *Abra alba*, *M. bidentata* and *L. conchilega* are species that typically occur in shallow fine sand areas but occur more frequently and in higher abundances in areas were *O. fusiformis* is present (in whatever densities). This is similar to what has been found for the sponge *Halichondria panicea*, where the associated species were also found in other habitats (Peattie and Hoare, 1981) and species richness also seems to be higher in areas with this sponge. These emergent ecosystem engineers are able to trap (mostly juveniles of) species because of changing hydrodynamics rather than enrichment through active movement of organisms (Savidge and Taghon, 1988).

## Owenia fusiformis *stabilizes dunes*

The results on the remote sensing imagery highlight the potential of using both multibeam and side-scan sonar to detect *O. fusiformis* aggregations. Both images show a patchy pattern. Degraer et al. (2008a) observed similar, though smaller patches on side-scan sonar images which corresponded with the occurrence of *L. conchilega* reefs (average surface of 4.4 m²). The latter were, on the contrary, not detected with the 95 kHz multibeam sonar, probable due to their smaller surface area compared to *O. fusiformis* aggregations. However, under favourable circumstances, *L. conchilega* reefs can be detected also with very-high resolution multibeam systems (e.g. > 300 kHz systems). Still, the delineation of individual *O. fusiformis* patches is not straightforward using sonar systems of 95 kHz only. Even terrain analysis, allowing obtaining further quantitative descriptors of the bathymetry data, did not solve this problem (Wilson et al., 2007). Although its superior qualities in small object detection, the lack of depth information does not allow delineating the patches based on the very-high resolution side-scan sonar imagery.

Nonetheless, the remote sensing tools have demonstrated clearly the stabilizing effects *O. fusiformis* aggregations have on the geomorphology of sand dunes. The dunes in the northern and central part of the study area did not migrate between February 2006 and November 2007, while in the south-western part of the study area, dunes moved 12 m towards the SW. A dune migration of 12 m to the SW is expected in the whole study area (Besio *et al.*, 2004, Degrendele *et al.*, in prep., Nemeth *et al.*, 2002). The absence of dune migration in the northern and central part could only be attributed to the stabilizing effect of *O. fusiformis*.

Sediment stabilization by *O. fusiformis* has been hypothesized before as an explanation for the temporal stability of the *A. alba- Pectinaria (Lagis) koreni* community in the Bay of Seine (Thiebaut et al., 1997).

Borsje et al. (2009b) have discussed in detail the biophysical interactions between benthos and their sedimentary environment. They argue that biota are able to impact on hydrodynamics (e.g. adding roughness to the bottom) and may induce flow deceleration within epibenthic structures. Accounting for biota in both sediment dynamics and hydrodynamics may produce results of several orders of magnitude difference and can act on a large spatial and temporal scale. The same authors demonstrate the influence of ecosystem engineers on both the wavelength and presence of bedforms, hence having a direct effect on the morphodynamics also. From this, it is clear that biota form an inherent component of models predicting seabed dynamics. These are increasingly important with the expansion of human activities in coastal zones. Data from this study aid in the parameterisation of biological activity on sandbank systems. Monitoring this area (3-4 times a year) would provide insight into its temporal dynamics.

## *Biotic stabilization*

The aggregations of *O. fusiformis* tubes might induce a "skimming flow", explaining the attraction of species preferring high mud content. However, Paarlberg et al. (2005) indicate that in general, stabilizing organisms can, but do not necessarily, cause an increase of mud content and additional sedimentation. Eckman et al. (1981) visualize the results of flume experiments (Nowell and Church, 1979) by representing the "critical" ratio between tube size and density that is critical to change from a destabilizing effect to a stabilizing one. In their experiments with *O. fusiformis*, they show that the maximum kinetic energy production and hence the maximum shear stress production occurs at the bed, which indicates that there is no skimming flow. Destabilization occurs at natural densities (as predicted from the produced ratio). They calculated that for *O. fusiformis* tube densities of below 13,000 ind /m² sediment destabilization will occur. However, a study with artificial tubes (Friedrichs et al., 2000) show a deceleration of current velocity with increasing tubes; they show that skimming flow conditions already occur at 8.8% surface coverage (*i.e.* 3836 tubes/m²). Also Fager (1964) notes that stable patches occurred (*i.e.* absence of ripples) with relatively low densities.

Therefore, the presence of the tubes built by *O. fusiformis* cannot by itself explain the bed stability that is demonstrated in this study with the remote sensing imagery. Eckman et al. (1981) suggest that alternative processes compensate for the destabilizing effect of the *O. fusiformis* tubes: production of mucus by bacteria, benthic diatoms, filamentous algae and sea grasses. Fager (1964) described a diatom film within *O. fusiformis* aggregations that was uncommon at similar depths outside the aggregations. Murray et al. (2002) suggest that the mucus produced by the invertebrate itself may play a major role in the geophysical properties of the sediment through flocculation, drag reduction, pore blockage or cementation. Present study demonstrates the high stabilization potential of the species. This stabilization effect is most probably the result of subsequent effects after tube settlement as average tube density was around 600 ind $m^{-2}$. The biological characteristics of the species are of importance: the combination of the long lifespan and the rigid tube make that this ecosystem engineer is able to have far reaching stabilizing effects in a highly dynamic environment. Nevertheless, compared to the relatively low densities needed to detect the biological impact of the ecosystem engineer, higher densities of the species are a key to create detectable large scale stabilization. Moreover, large-scale effects of small-scale biological activity by stabilizing organisms are mainly responsible for the seasonal variation in suspended sediment concentrations (Borsje *et al.*, 2009a, Borsje *et al.*, 2008). Adults occur mainly as dense patches within fine and muddy sand (Barnay et al., 2003) and have been recorded off Helgoland Island in the North Sea (Noffke et al., 2009), in the English Channel (Dauvin and Gillet, 1991) and in the Mediterranean Sea (Pinedo et al., 2000). In present study, the influence of high nutrient supply of the Scheldt estuary is probably a driving force to have high density patches. Aggregations of *O. fusiformis* are generally stable but can disappear as a consequence of changing abiotic factors (such as harsh winters or reduced food supply) (Dauvin and Gillet, 1991, Noffke *et al.*, 2009).

Ground truth samples show average tube densities of over 500 ind/$m^2$, suggesting that relatively high densities are needed to have a clear stabilizing effect, compared to the relatively low densities needed to reach maximum biological effects.

## *Implications for management*

Ecosystem engineers can extend a species range towards environments the species would otherwise physically have more difficulties to inhabit. Important ecosystem engineers alleviate limiting abiotic and biotic stresses, expanding distributional limits for numerous species, and often create the foundation for community development. As the management of important engineers can protect numerous associated species and functions, it has been advocated to use these organisms as conservation targets (Crain and Bertness, 2006). This will necessitate a shift towards a more process-based understanding of the functioning of systems; an important step towards ecosystem-based management (Byers et al., 2006). Present study demonstrates that for the marine environment, combining biological data analyses with remote sensing imagery provides more process-based insight in the benthic microhabitat that is created by *O. fusiformis*. Therefore, this study generates an opportunity to implement the ecosystems approach in this particular area.

Byers et al. (2006) developed a conservation framework that uses the ecosystem engineer concept. These authors argue that ecosystem engineers are often likely to be the causative agents, driving the transition between alternative system states. Although in their model they emphasize on non-trophic engineering effects, they also stress on the important and often interacting role of trophic and other biological interactions in restoration. The ecosystem engineer concept should therefore be considered as a contributory process among those factors affecting the distribution and abundance of organisms and the functioning of ecosystems (Wright and Jones, 2006). Present study qualifies the tube building polychaete *O. fusiformis* as an important ecosystem engineer. Results show that this species is able to modulate its environment in such a way that physical structures as large as sand dunes can be stabilized. The stabilizing function of benthic biota taken together with the increased ecological richness, make these environments of particular interest for future management schemes.

Anthropogenic impacts that affect benthic tube worm aggregations, such as towed bottom-fishing gear, can pose a significant threat to the integrity of complex benthic habitats, particularly those formed by sessile emergent fauna (Collie *et al.*, 1997, Kaiser *et al.*, 2000b, Rabaut *et al.*, 2008, Thrush *et al.*, 1998, Watling and Norse, 1998). Traditionally, fisheries

managers have been preoccupied with the conservation of single stocks of target species, giving little or no consideration to the secondary effects of fishing on the marine ecosystem (Kaiser *et al.*, 2000b). Damage to the stabilized *O. fusiformis* habitat may not only cause reduced macrobenthic (prey) abundance (*cf.* e.g. possible effects on the associated species), but also an ecosystem change from a stabilized dune habitat towards a highly dynamic habitat with migrating dunes.

Moreover, the study area of present research (the "Vlakte van de Raan") is situate d in the eastern side of the BPNS and constitutes an area of high biological value (Derous, 2007). The area was partially designated as a Special Area for Conservation in the framework of the EC Habitats Directive, but has been annulled by the Council of State because of insufficient motivation after a complaint against the designation by an energy firm (Cliquet *et al.*, 2008b). Present study emphasizes the ecological importance of this particular area and can serve as a motivation to reconsider this particular area. The identification and subsequent quantification of the value of specific ecosystem engineers are considered as important steps in the strategy to implement the ecosystems approach in the marine environment (Rabaut *et al.*, 2009c).

## Conclusions

*Owenia fusiformis* proves to be an ecosystem engineer that stabilizes sand bank systems and has clear consequences for the biotic (benthic) community structure that profits form a stable small scale niche in an otherwise highly dynamic area. Aggregations of *O. fusiformis* can be mapped with both multibeam echosounder and side-scan sonar technology. The detectability of an enriched ecosystem engineered habitat provides opportunities to implement a sustainable management regime. Moreover, results emphasize that biota – especially ecosystem engineers- should be included in hydrodynamic sediment transport modelling. The present study proves that remote sensing techniques permit to improve the knowledge of marine biodiversity, its spatial distribution and its biophysical impact in a cost-effective way.

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